

The morphological phylogeny of the family Protoschizomidae revisited (Arachnida: Schizomida): setal characters, fossil and paraphyletic genera

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Abstract. The schizomid family Protoschizomidae, endemic to North America, is represented by two genera and 15 species. While most of the species are distributed in caves in the Sierra Madre Oriental system in Mexico; other species are found in caves in the Sierra Madre Occidental system. Recently, a new species of this family was described from a cave in the Mexican Trans-Volcanic Belt, representing the linking bridge between both Sierras. In the present contribution, we propose a new nomenclature of the pedipalp setae of the protoschizomids. We revise the phylogenetic status of Protoschizomidae using 137 morphological characters (including the proposed pedipalp setae) and 7 outgroup taxa using parsimony criteria. Based on our results, Protoschizomidae was recovered as monophyletic, but the monophyly of *Protoschizomus* Rowland, 1975 was not recovered because of the inclusion of *Agastoschizomus* Rowland, 1971 and the fossil *Onychothelphynus bonneri* Pierce, 1951. Therefore, we transfer the genus *Onychothelphynus* Pierce, 1951 and species *O. bonneri* to this family, but other taxonomical changes were not considered.

Keywords: Pedipalp setae, parsimony, fossil

The family Protoschizomidae Rowland, 1975, a relatively small, distinctive group of schizomids (Fig. 1), is currently represented by two genera and 15 species mainly distributed in Mexico (Harvey 2003; Prendini 2011; Monjaraz-Ruedas 2013; Monjaraz-Ruedas et al. 2016a; listed in Table 1), with some specimens reported from Texas (Cokendolpher & Reddell 1992; Reddell & Cokendolpher 1995; Monjaraz-Ruedas et al. 2016a). The family was originally described by Rowland (1975) to accommodate the newly created genus *Protoschizomus* Rowland, 1975, and to transfer the genus *Agastoschizomus* Rowland, 1971, previously assigned to the subfamily Megaschizominae Rowland, 1973 (see Cokendolpher & Reddell 1992). *Protoschizomus* currently contains four troglobitic species and three epigeal species, whereas *Agastoschizomus* is represented by eight strictly troglobitic species (Monjaraz-Ruedas 2013; Monjaraz-Ruedas et al. 2016a).

The distribution of both genera is quite interesting. Even though most of the species are found in cave systems in the Sierra Madre Oriental, they don't follow the same pattern of distribution as other arachnids found in the same mountain system (in the Mexican states of Hidalgo, San Luis Potosí, Oaxaca, Tamaulipas and Veracruz), such as species of scorpion genus *Typhlochactas* Mitchell, 1971 (Vignoli & Prendini 2009); species of several opilionid genera such as *Karos* Goodnight & Goodnight, 1944 and *Chapulobunus* Goodnight & Goodnight, 1946 (Cruz-López & Francke 2015); or pseudoscorpion species in the genus *Typhloroncus* Muchmore, 1979 [although this genus is also represented by a species in the Virgin Islands (Harvey & Muchmore 2013)]. So far there are no reports of species of protoschizomids in the Sierra Madre Oriental, south of the Mexican Trans-Volcanic Belt in the states of Oaxaca, Puebla and Veracruz. However, there are three species of protoschizomids in the Sierra

Madre Occidental in Guerrero and Colima (Montaño-Moreno & Francke 2009; Monjaraz-Ruedas 2013; see Fig. 2); and recently our team described a new species of *Agastoschizomus* from Estado de México, which represents a biogeographic bridge in the Mexican Trans-Volcanic Belt (Morrone 2005) joining the distribution of these species in those two branches of the Sierra Madre (Monjaraz-Ruedas et al. 2016a).

Previous phylogenetic analyses.—Cokendolpher & Reddell (1992) tested the monophyly of the family using a cladistic analysis of morphological traits. Their analysis, based on 14 taxa and 43 characters, had two purposes: first to investigate the relationship of the orders Thelyphonida and Schizomida; and second, the relationships of the members of the family Protoschizomidae. The monophyly of the family was supported by five synapomorphies: (1) a pair of setae at the base of the anterior process; (2) the pedipalps without sexual dimorphism; (3) female flagellum without annuli; (4) flagellar setal pattern different in both sexes; and (5) the male flagellum without distinct stalk (Cokendolpher & Reddell 1992). *Agastoschizomus* was supported by five synapomorphies and *Protoschizomus* was supported by three (see fig. 2 in Cokendolpher & Reddell 1992).

In the same contribution, Cokendolpher & Reddell (1992) proposed two species groups within *Protoschizomus*: the “*pachypalpus*” group (*P. pachypalpus* (Rowland, 1973), *P. rowlandi* Cokendolpher & Reddell, 1992 and *P. occidentalis* Roland, 1975) and the “*sprousei*” group (*P. sprousei* Cokendolpher & Reddell, 1992 and *P. purificacion* Cokendolpher & Reddell, 1992). The “*pachypalpus*” group was supported by four characters (two anteriorly placed setae pairs present in the dorsal propeltidium; the male pedipalps longer than the body length; the tergite III with four setae and the

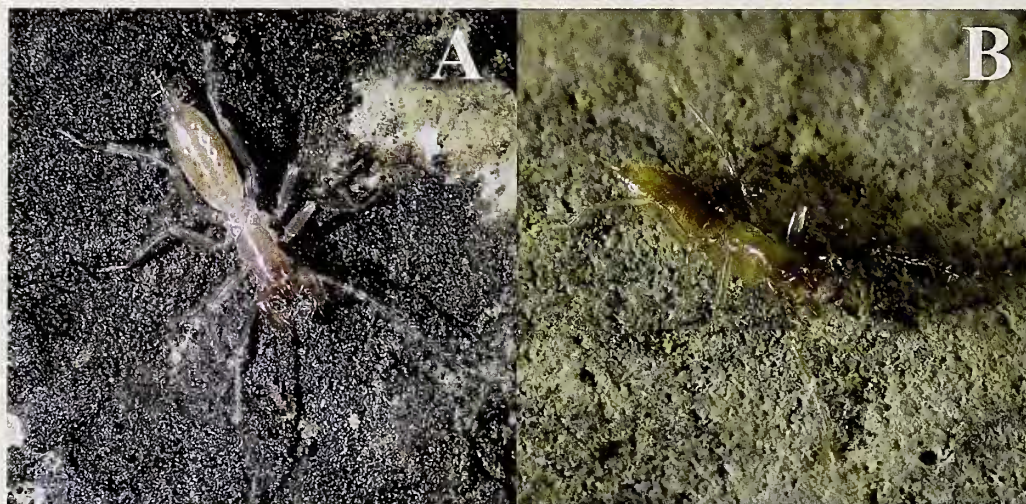


Figure 1.—Species representatives of the family Protoschizomidae. A. *Protoschizomus tenebris*. B. *Agastoschizomus texanus*, photo by Jean Krejca.

receptaculum margins smooth with pits, see Cokendolpher & Reddell 1992); whereas the “*sprousei*” group was supported only by two characters (the pedipalp trochanter slightly produced, and the absence of *Dm4* seta on the female flagellum). Also, *Agastoschizomus* was recovered as monophyletic as an unresolved polytomy (Cokendolpher & Reddell 1992; their fig. 2).

In a recent contribution, Monjaraz-Ruedas et al. (2016b) revised the ancestral state of the schizomid female flagellum annuli, and the homology of the flagellum setae across Protoschizomidae and Hubbardiidae. The monophyly of Protoschizomidae was not recovered using only those characters proposed by Cokendolpher & Reddell (1992). However, new observations on the pedipalp setae (Monjaraz-Ruedas, unpublished data; this contribution) provided additional characters to explore this problem in the systematics of Protoschizomidae.

The status of *Onychothelyphonus bonneri*.—Arachnid fossils are abundant and all of the extant orders are represented by fossil species. Several schizomid fossils are known: (a) the family Calcitronidae Petrunkevitch, 1945 contains one genus and two fossil species, one from the U.S.A. (Pliocene) and one from China (Oligocene), (b) and two monotypic genera assigned to the family Hubbardiidae, subfamily uncertain, *Calcoschizomus* Pierce, 1951 (Pliocene, U.S.A.) and *Onychothelyphonus* Pierce, 1951 (Pliocene, U.S.A.) (Harvey 2003). Published illustrations of *Onychothelyphonus bonneri* Pierce, 1951 (Pierce 1951; Petrunkevitch 1955; Dunlop & Penney 2012) suggest that this fossil actually belongs in the family Protoschizomidae and, for that reason, we included it in the phylogenetic analyses below.

In the present contribution, we propose a nomenclature for the setae found on the pedipalp femur, patella and tibia of protoschizomids; and we include those characters in a

Table 1.—Listed species currently recognized in family Protoschizomidae. *Indicates fossil taxa

Genus	Distribution	Habitat
<i>Agastoschizomus</i> Rowland, 1971		
<i>A. huitzmolotlensis</i> Rowland, 1975	San Luis Potosi, Mexico	Hypogean
<i>A. juxtlahuacensis</i> Montaña-Moreno & Francke, 2009	Guerrero, Mexico	Hypogean
<i>A. lucifer</i> Rowland, 1971	San Luis Potosi, Mexico	Hypogean
<i>A. patei</i> Cokendolpher & Reddell, 1992	Tamaulipas, Mexico	Hypogean
<i>A. stygius</i> Cokendolpher & Reddell, 1992	Hidalgo, Mexico	Hypogean
<i>A. tamaulipensis</i> Monjaraz-Ruedas, Francke & Cokendolpher, 2016	Tamaulipas, Mexico	Hypogean
<i>A. tenebris</i> Monjaraz-Ruedas, Francke & Cokendolpher, 2016	Tamaulipas, Mexico	Hypogean
<i>A. texanus</i> Monjaraz-Ruedas, Francke & Cokendolpher, 2016	Texas, United States	Hypogean
<i>Onychothelyphonus</i> Pierce, 1950*		
<i>O. bonneri</i> Pierce, 1950*	Arizona, United States	Unknown
<i>Protoschizomus</i> Rowland, 1975		
<i>P. franckei</i> Monjaraz-Ruedas, 2013	Guerrero, Mexico	Hypogean
<i>P. gertschi</i> Cokendolpher & Reddell, 1992	Tamaulipas, Mexico	Hypogean
<i>P. occidentalis</i> Rowland, 1975	Colima, Mexico	Epigean
<i>P. pachypalpus</i> (Rowland, 1973)	Tamaulipas, Mexico	Epigean
<i>P. purificacion</i> Cokendolpher & Reddell, 1992	Tamaulipas, Mexico	Hypogean
<i>P. rowlandi</i> Cokendolpher & Reddell, 1992	San Luis Potosi, Mexico	Epigean
<i>P. sprousei</i> Cokendolpher & Reddell, 1992	Tamaulipas, Mexico	Hypogean

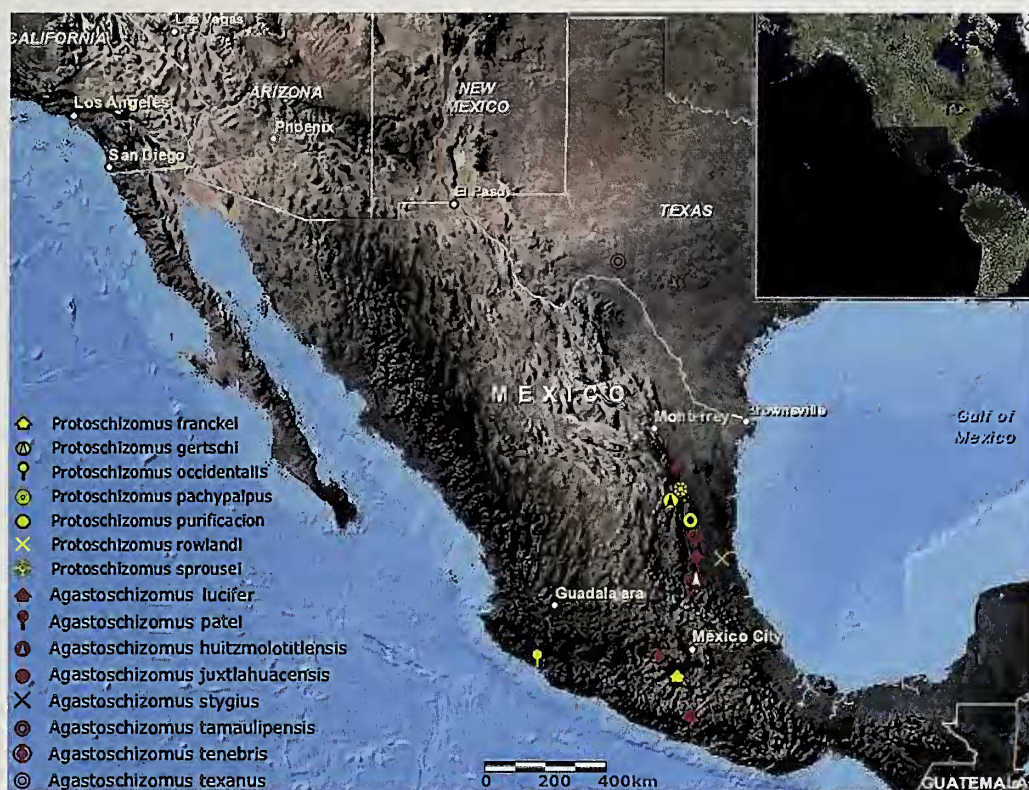


Figure 2.—Distribution map of the extant species of the family Protoschizomidae.

phylogenetic analysis using 15 species of the family Protoschizomidae as the in-group: seven species of genus *Protoschizomus* (*Protoschizomus treacyae* Cokendolpher & Reddell, 1992 represents a junior synonym of *P. purificacion*, new synonymy; see below), and the eight described species of genus *Agastoschizomus*. As out-groups, we included the fossil *O. bonneri* and seven exemplar species, representing five genera of the subfamily Hubbardiinae (Hubbardiidae), and *Megaschizomus mossambicus* (Lawrence, 1958) of the subfamily Megaschizominae (Hubbardiidae) to root our topologies. The matrix contains 137 morphological characters: 65 characters from pedipalp setae, 25 characters from males, and 30 characters from females only. Analyses were conducted with parsimony under equal and three implied weighting regimes. Unfortunately, efforts to collect fresh tissues of these animals to obtain molecular data have been unsuccessful in the past 10 years. This is not rare because until today, only one schizomid molecular phylogeny has been published (Harvey et al. 2008). Until this becomes possible, the branch support values here reported were not considered significant enough to make the necessary taxonomical changes.

METHODS

Taxa.—Material examined is deposited in the following collections: American Museum of Natural History, New York (AMNH), and in the Colección Nacional de Arácnidos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (CNAN), and it is listed in Appendix 1.

Observations were made using Nikon SMZ-800 and SMZ-1500 stereomicroscopes, and a Nikon Eclipse E100 optical

microscope. Measurements (mm) follow Cokendolpher & Reddell (1992), and were obtained with an ocular micrometer calibrated at 10x. Morphological terminology follows Cokendolpher & Reddell (1992), except for cheliceral setae (Lawrence 1969), flagellar setae terminology (Monjaraz-Ruedas et al. 2016b) and pedipalp setae terminology (see below).

Drawings were copied from digital images taken under visible light with a Nikon Coolpix S10 VR camera attached to a Nikon SMZ-800 microscope. The focal planes of image stacks were fused with CombinedZM (Hadley 2008), composite images were edited with Adobe Photoshop CS6, and drawings edited with Adobe Illustrator CS6.

Pedipalp setal nomenclature.—There are four kinds of setae (Figs. 3, 4): (a) acuminate setae, present on most of the genera of the family Hubbardiidae (Fig. 3A–D); (b) macrosetae (Fig. 3E, F), that are present only in the family Protoschizomidae, and are the equivalent of acuminate setae of hubbardiids but longer and wider than said acuminate setae; (c) feathered setae, present primarily on the pedipalp tibia (Fig. 4); (d) spiniform setae, which are dark, thickened setae with an evident socket and strongly sclerotized, and that are very common in genus *Hubbardia* Cook, 1899 and on Protoschizomidae (Fig. 4).

Setal patterns and setal forms were examined on all segments of the pedipalp in search of phylogenetically informative characters. In this contribution, we consider and describe: (a) the setae present on ectal and mesal surfaces of the femur, (b) the setae present on the ventral surface of the patella, and (c) the setae present on the ventro-mesal surface of the tibia. Seta numbering on each surface is performed from basal to distal position of the segment.

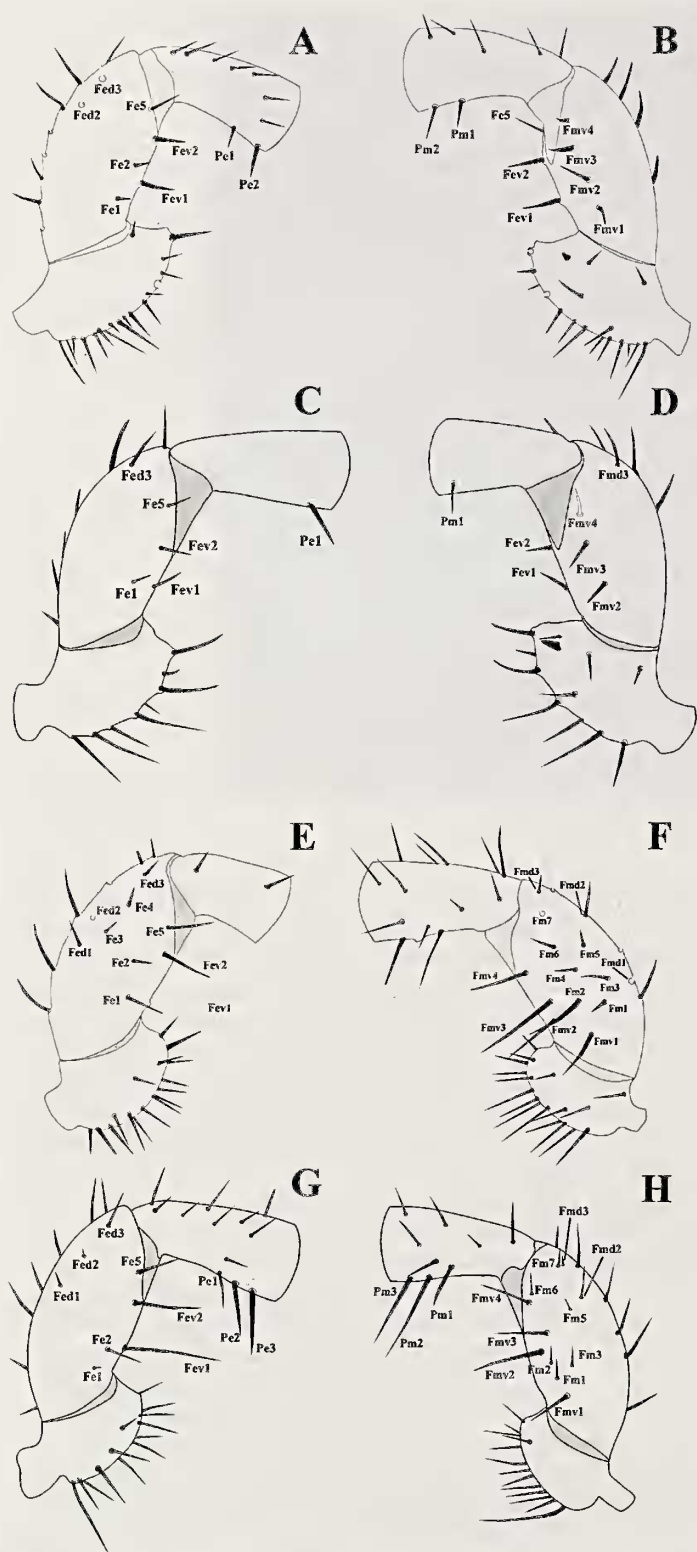


Figure 3.—Setal pattern of the pedipalp femur of Schizomida. *Hubbardia pentapeltis*: A. Femur ectal view. B. Femur mesal view. *Stenochrus peckii*: C. Femur ectal view. D. Femur mesal view. *Agastoschizomus juxtlahuacensis*: E. Femur ectal view. F. Femur mesal view. *Protoschizomus franckei*: G. Femur ectal view. H. Femur mesal view.

Setae are named based on position (Segment and surface of the pedipalp), with capital letters indicating the different segments of the pedipalp and lower case letters indicating surface or position: *Fe* = femur ectal, *Fed* = femur ectal dorsal, *Fev* = femur ectal ventral, *Fm* = femur mesal, *Fmd* = femur mesal dorsal, *Fmv* = femur mesal ventral; *Pe* = patella ectal, *Pm* = patella mesal, *Pmm* = patella medial mesal, *Pme* = patella medial ectal and *Ter* = tibia external row, *Tmr* = tibia medial row, *Tir* = tibia internal row, *Tm* = tibia medial.

The pedipalp femur of protoschizomids, in general presents more setae than the femur of hubbardiids: protoschizomids (Fig. 3A, C) possess on ectal face 1-3 ecto-dorsal setae (*Fed*), more than three ectal setae (*Fe*) and one pair of ecto-ventral setae (*Fev*), whereas hubbardiids (Fig. 3E, G) present only two ecto-dorsal setae, three ectal setae and one pair of ecto-ventral setae. On the mesal surface of the pedipalp femur, hubbardiids (Fig. 3F, H) possess only a meso-ventral row of three or four setae (*Fmv*), whereas protoschizomids (Fig. 3B, D) possess dorsal (*Fmd*), mesal (*Fm*), and meso-ventral setae (*Fmv*), the number of setae in each group varies among species and is phylogenetically informative within the family (see Appendix 2).

The patella possesses two ill-defined rows of setae (Fig. 4): one on the ventro-ectal margin (*Pe*) and one on ventro-mesal margin (*Pm*); hubbardiids usually have only acuminate setae on the patella (Fig. 4E–H), whereas protoschizomids tend to have macrosetae (Fig. 5A–D). Setae *Pmm* and *Pme* vary among species of Protoschizomidae, however, in Hubbardiidae, the setae *Pme1* and *Pmm3* are always present (see Fig. 5C, E).

The tibia possesses three distinct rows of setae on the ventral and the ventro-mesal surface on both families: the external row (*Te*) usually possesses three setae on hubbardiids and seven setae on protoschizomids; the medial and internal rows possess four setae on hubbardiids and five on protoschizomids, which also present an extra pair of setae *Tm*, located medially, near medial row and distal margin (Fig. 4). The number of setae and the shape of the setae (acuminate, feathered or spiniiform) of all segments is diagnostic to species level and of phylogenetic importance at the generic level.

Data matrix.—One hundred and thirty-seven qualitative characters of adult morphology (Appendix 2) were scored (Appendix 3) for the 23 terminal taxa in the analysis using museum material. Forty-seven characters were multistate and 90 binary. Twenty-five characters were scored only for males, and 30 were scored only for females. Adult females are unknown in *Agastoschizomus huitzmolotitlensis* Rowland, 1975 and *Agastoschizomus juxtlahuacensis* Montañó-Moreno & Francke, 2009; whereas adult males are unknown in *P. gertschi* Cokendolpher & Reddell, 1992, *P. purificacion* (sub adult male), *A. stygius* Cokendolpher & Reddell, 1992 and *A. texanus* Monjaraz-Ruedas, Francke & Cokendolpher, 2016. *Onychothelyphonus bonneri* was coded from the literature (Pierce 1950; Petrunkevitch 1955; Dunlop & Penney 2012).

Sixty-five characters were scored from setal patterns in the pedipalp trochanter, femur, patella and tibia; and forty-three characters are coded from the flagellum. Seven characters were uninformative and deactivated in all parsimony analyses († in Appendix 2).

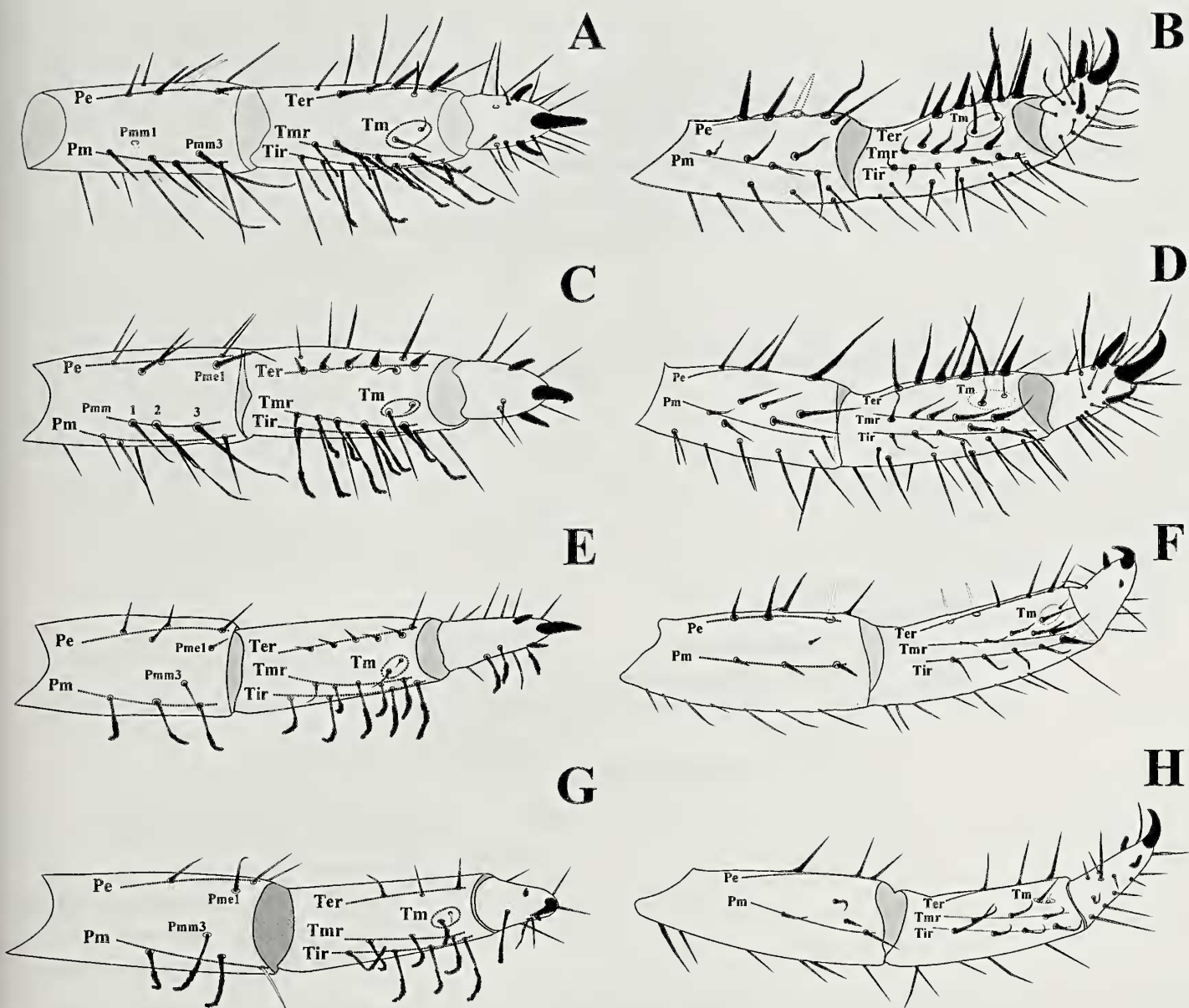


Figure 4.—Setal patterns of the pedipalp patella and tibia of Schizomida. *Agastoschizomus juxtlahuacensis*: A. ventral view. B. Mesal view. *Protoschizomus franckei*: C. Ventral view. D. Mesal view. *Hubbardia pentapeltis*: E. Ventral view. F. Mesal view. *Stenochrus pecki*: G. Ventral view. H. Mesal view. Feathered setae = Tibia internal and medial rows (Tir and Tmr); spiniform setae = Tibia external row (Ter).

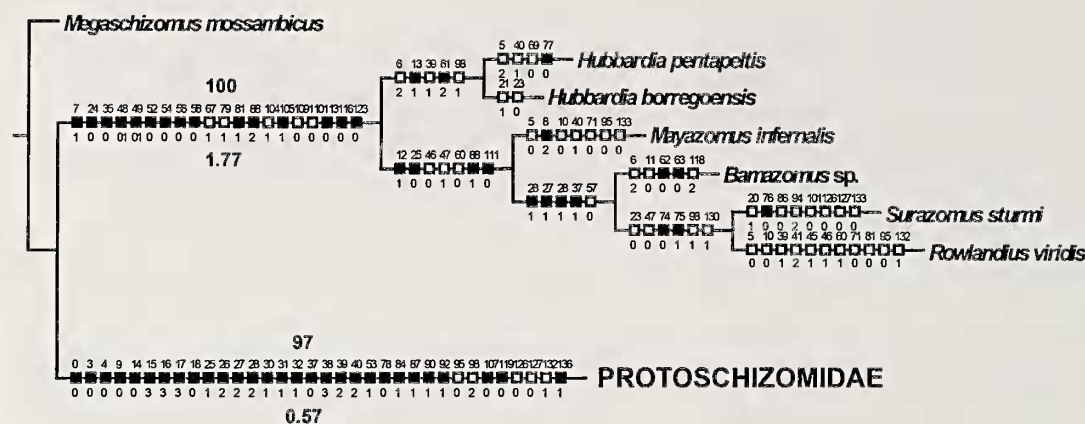
Parsimony phylogenetic analyses.—A driven search of the 130 informative characters was conducted in TNT (Goloboff et al. 2003a,b, 2008) combining three of the new technology algorithms (Goloboff 1999; Nixon 1999) executed using a script file modified from Dimitrov et al. (2013) and Santibáñez-López et al. (2014): *hold 100000; rseed1; xm: noverb nokeep; rat: it 0 up 4 down 4 au 0 num 36 give 99 equa; dri: it 10 fit 1.00 rfi 0.20 aut 0 num 36 give 99 xfa 3.00 equa; sec: mins 45 maxs 45 self 43 incr 75 minf 10 god 75 drift 6 glob 5 dglob 10 rou 3 xss 10- 14+2 noxev noeq; tf: rou 5 minf 3 best ke nochoo swap; xm: level 10 nochk rep 50 fuse 3 dri 10 rss css noxss mult nodump conse 5 conf 75 nogive notarg upda autoc 3 xmix; xm: xmult:.* Analyses were carried out with equal weighting and implied weighting using three values of the concavity constant ($k = 1, 3, 10$), to assess the effect of weighting against homoplastic

characters. The relative support for each node on the preferred hypothesis was calculated with Bremer support (Bremer 1994) and jackknife resampling (Farris et al. 1996). Bremer support was calculated in TNT by searching for suboptimal trees 10 steps longer, and holding 1000 trees per replication, using the command *bremer*;. Jackknife support was estimated with heuristic searches of 1000 pseudoreplicates, using the commands *resample jak repl*;. Cladograms were generated with WinClada (Nixon 2002) and edited with Adobe Illustrator C6.

RESULTS

Based on the revision of the holotypes of *Protoschizomus treacyae* and *P. purification* (both females), we concluded that in the original description by Cokendolpher & Reddell (1992), the diagnostic characters were not correctly observed. These

A



B

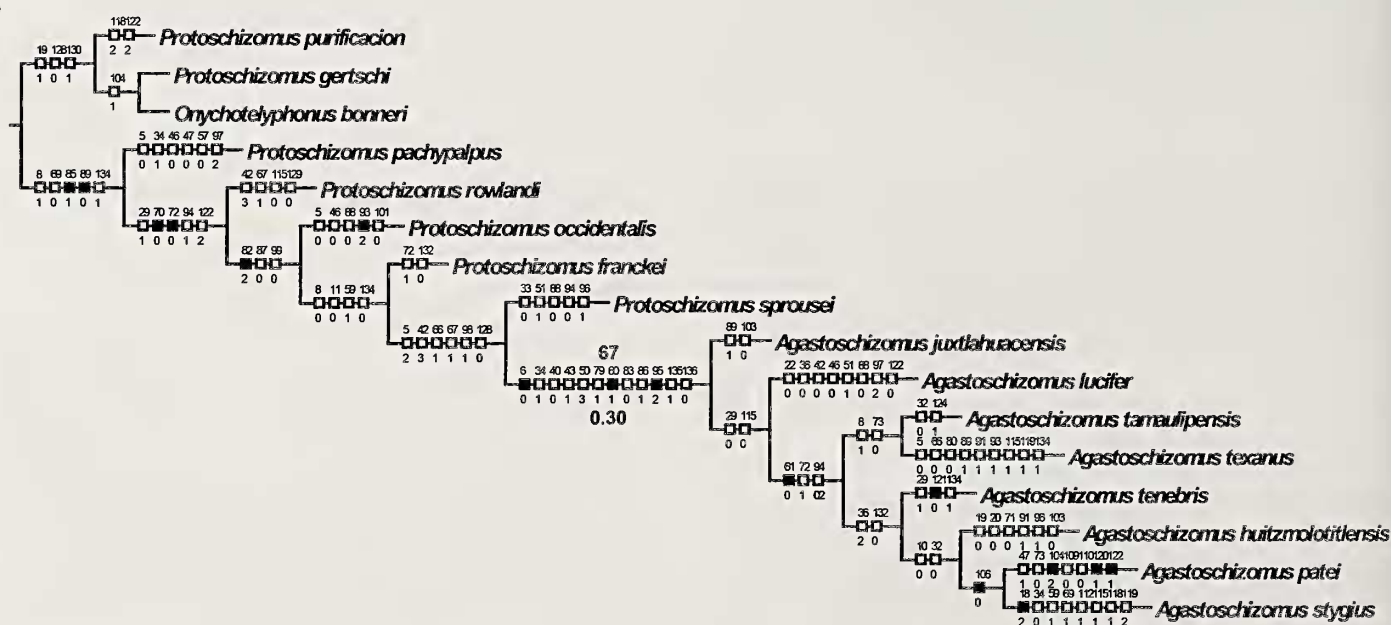


Figure 5.—The single most parsimonious tree obtained from the cladistic analysis of 137 morphological characters scored from 23 species in 9 schizomid genera with implied weighting and k value = 3. Unambiguous synapomorphies optimized on branches: black squares indicate apomorphic states, while white squares indicate either parallel derivations of apomorphic characters or reversal to plesiomorphic states; numbers above squares indicate characters, numbers below indicate states. Jackknife values greater than 65% indicated above branches. Bremer support values indicated below branches. A. Monophyly of Protoschizomidae. B. Internal relationships within Protoschizomidae.

authors differentiated *P. treacye* from *P. purification* as follows: *Dm2* on female's flagellum is absent in *P. treacye*, but it is present in *P. purification*; the segment/article 5 in female's flagellum is present in *P. treacye*, but absent in *P. purification*. However, seta *Dm2* is also absent in *P. purification*; and recently, Monjaraz-Ruedas et al. (2016b) proposed new terminology for the segments/articles in schizomids ("flagellomere" and "annuli"); therefore, both species have the flagellomere 5. In addition to this, we compared the spermathecae of both species and they are similar. Therefore, *P. treacye* is now considered a synonymy of *P. purification* (new synonym).

Phylogenetic analyses of family Protoschizomidae.—The analysis with equal weighting and with implied weighting using three values of k (1, 3, 10) recovered the monophyly of

family Protoschizomidae. Our preferred topology was the one obtained from the analysis with implied weighting and k value = 3 because of its tree statistics (Table 2) and the branch support values for the clades recovered (Jackknife and Bremer). In this topology, the family Protoschizomidae was supported by 29 synapomorphies (22 from pedipalp setae characters, Figs. 5, 6) and five homoplastic characters; and with high support values of jackknife and Bremer values (Fig. 5). Despite the great number of synapomorphies supporting the family, the relationships within Protoschizomidae were not resolved.

The genus *Protoschizomus* was never recovered as monophyletic due to the terminal placement of *Agastoschizomus*, which was recovered monophyletic (but with low branch support values); and due to the inclusion of the fossil

Table 2.—Tree statistics from the most parsimonious trees or the consensus trees (*) obtained from cladistic analyses of 23 species in 9 schizomid genera. MP = Most parsimonious trees, L= Length, CI= Consistency Index, RI= Retention index, FIT= Fit, AH= Adjusted Homoplasy, EW= Equal weighting, IW= Implied weighting.

		MP	L	CI	RI	FIT	AH
EW		6	378*	0.487*	0.711*	97.04*	—
IW	k=10	1	371	0.496	0.721	115.54	14.46
IW	k=3	1	371	0.496	0.721	97.09	32.91
IW	k=1	1	374	0.492	0.717	75.97	54.03

Onychothelyphonus bonneri. The phylogenetic position of *Onychothelyphonus bonneri* (supported by the absence of the mesal spur in the pedipalp trochanter; the absence of the annulus ‘b’ in the female’s flagellum and the position of the seta *D13* in relation to *V12*) suggests close relationships with extant protoschizomids, rather than being an extinct member of family Hubbardiidae (with which it shared only the size of the female’s flagellum, char 105; see below).

The genus *Agastoschizomus* was recovered monophyletic supported by three synapomorphies (one seta on the anterior process of the propeltidium, the femur of leg IV more than 4.8

times longer than deep, and the male’s flagellum seta *D13* anterior to *V12*) but with low jackknife support (70%). There was no internal resolution within *Agastoschizomus* because the species’ relationships had no branch support values.

DISCUSSION

Phylogenetic position of *Onychothelyphonus bonneri*.—Scoring morphological traits for the fossil terminal for a matrix this size might have resulted in a dubious phylogenetic position. Wiens (2003) mentioned that the number of characters scored for terminals like this is critical for its

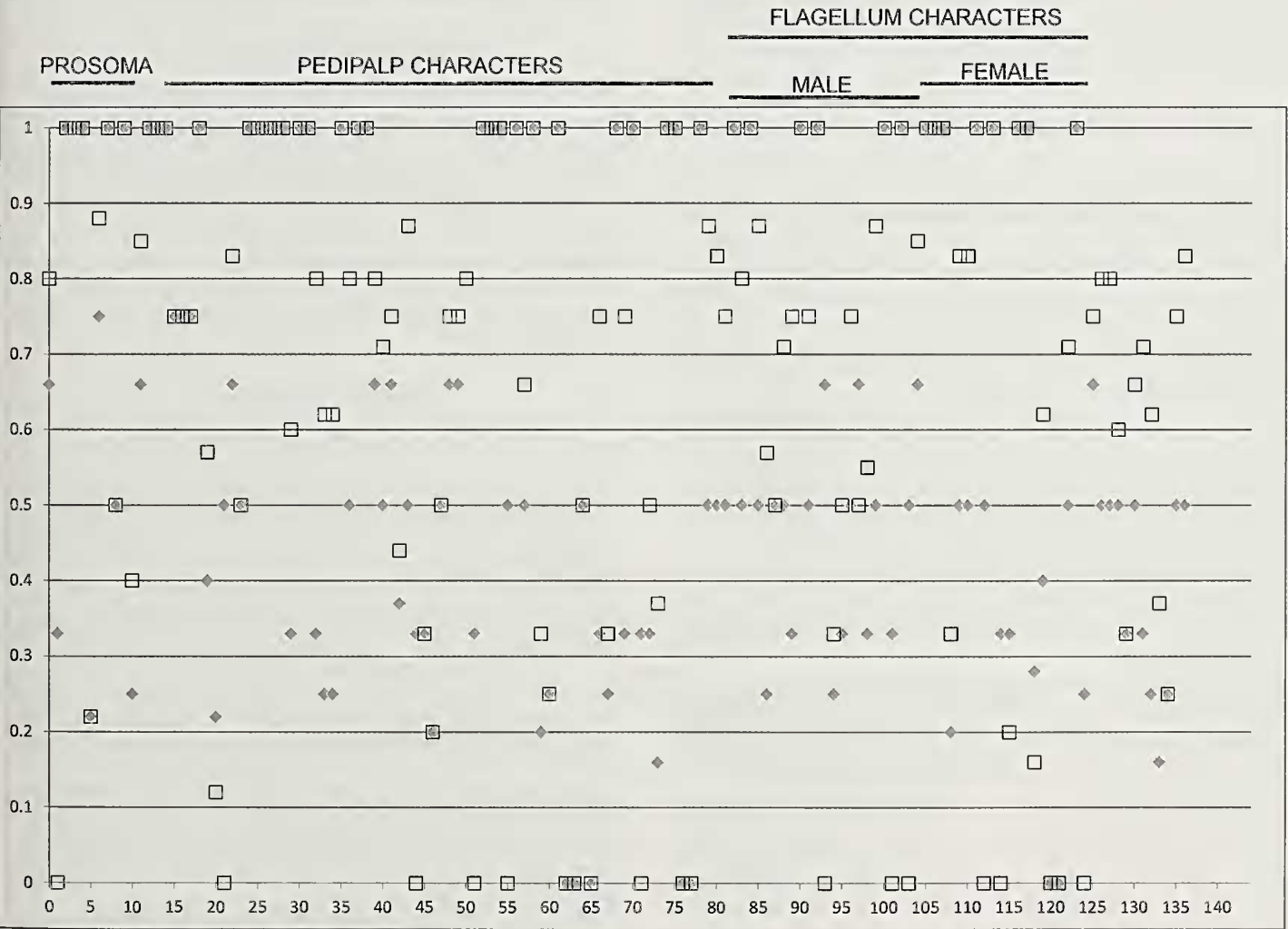


Figure 6.—Consistency indices (CI, gray diamonds) and retention indices (RI, white squares) of 137 morphological characters used in the cladistic analysis of 23 schizomid taxa, including all species of the family Protoschizomidae, the fossil *Onychothelyphonus bonneri* and several species of the family Hubbardiidae as outgroup.

“correct” phylogenetic position. He also mentioned that the insufficient sampling of characters in an incomplete taxon may lead to poor accuracy, both through incomplete resolution, and by increasing the chances that the taxon is spuriously placed on the tree by one or more homoplastic characters (Wiens 2003). However, how many characters are necessary to establish a fossil taxon’s correct phylogenetic position? According to Wiens (2003), in theory only a single character may be necessary, but increasing the number of characters sampled increases the probability that such a key character will be found.

We consider it is possible to observe “those necessary characters” to include *Onychothelyphonus bonneri* in the family Protoschizomidae: (1) absence of mesal spur, (2) trochanter IV about ½ length of femur IV, (3) female flagellum with seta *Dm3*, (4) female flagellum with seta *D11*, (5) female flagellum seta *D13* at same level as *V12*, (6) female flagellum with four annuli.

The phylogenetic relationship of *O. bonneri* with the extant protoschizomids would certainly not represent a surprise, given the young age of the fossil deposits (Pliocene 1.8 to 5.3 my), as suggested by Dunlop and Penney (2012). However, in our current database, in which *O. bonneri* is missing 131 characters, we can’t assure that this species represents an extinct species of genus *Protoschizomus*, or in any case, to put into synonymy this genus under *Onychothelyphonus* (by the principle of precedence); but it certainly represents a member of the family Protoschizomidae and not of Hubbardiidae where it is currently placed. Therefore, we transfer genus *Onychothelyphonus* and the species *O. bonneri* to family Protoschizomidae (new familial assignment).

Interestingly, all analyses recovered the following clade: ((*P. purificacion* + (*P. gertschi* + *O. bonneri*)). This relationship was supported by three homoplastic characters (chars 19, 128, 130; see Fig. 5 and Appendix 2); but with low support values. This relationship has not been recovered before (i.e., Cokendolpher & Reddell 1992).

Status of the two genera within Protoschizomidae.—The genus *Protoschizomus* was not recovered monophyletic nor were the two species groups as in the analysis of Cokendolpher & Reddell (1992). Those authors recovered the monophyly of *Protoschizomus* supported by three characters: trochanter IV about ½ length of femur, sternite VI short, and the male’s flagellum expanded distally (unknown in *P. gertschi*, *P. purificacion* (sub adult male), *A. stygius* and *A. texanus*). We modified their trochanter IV character into two characters: the ratio of trochanter length: width, and the ratio of trochanter length: propeltidium width (chars 79 & 80 respectively, see Appendix 2); both of which didn’t support the monophyly of *Protoschizomus*. In our analyses, the “sternite VI short” character was recovered as a synapomorphy for the family Protoschizomidae, but with a reversal in *Agastoschizomus* (char 136 in Fig. 5). Finally, the “male flagellum expanded distally” character (our char 83) is the plesiomorphic condition (absent in *Agastoschizomus*), because it is present in all hubbardiids studied here, and in all but the two species of *Protoschizomus* for which the male is unknown.

In the analysis of Cokendolpher & Reddell (1992), *Agastoschizomus* was supported by five synapomorphies, but with no internal resolution. In our analyses, three of those five

synapomorphies were recovered, whereas one character (our char 135) was recovered as a regression (because it was shared with the hubbardiids studied here), and the other character (our char 89) is a potential synapomorphy for the family (it is unknown in two *Protoschizomus* species and in *Onychothelyphonus bonneri*).

Traditionally, genus *Protoschizomus* is differentiated from *Agastoschizomus* based on the adult body size and by the presence of two setae in the anterior process of the propeltidium. Body size is no longer a good character because *A. texanus* is a small species. In our analysis, the presence of those setae was recovered as the plesiomorphic state (char 6 state 0) in *Protoschizomus* (shared with *Surazomus sturmi* (Kraus, 1957), *Rowlandius viridis* (Rowland & Reddell, 1969) and *Mayazomus infernalis* (Rowland, 1975)) and as a synapomorphy for *Agastoschizomus* (char 6 state 1). Therefore, this character remains as the most reliable to diagnose both genera as presently recognized. Unfortunately, molecular data are still missing for almost all protoschizomid species; and until this information becomes available to compare different phylogenetic hypotheses (which may provide better branch support values and better internal resolution), the necessary taxonomical arrangements should wait.

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LITERATURE CITED

- Bremer, K. 1994. Branch support and tree stability. *Cladistics* 10:295–304.
- Cokendolpher, J.C. & J.R. Reddell. 1992. Revision of the Protoschizomidae (Arachnida: Schizomida) with notes on the phylogeny of the order. *Texas Memorial Museum of Speleology Monographs* 3:31–74.
- Cruz-López, J.A. & O.F. Francke. 2015. Cladistic analysis and taxonomic revision of the genus *Karos* Goodnight and Goodnight, 1944 (Opiliones, Laniatores, Stygnopsidae). *Zoological Journal of the Linnean Society* 175:827–891.
- Dimitrov, D., J.J. Astrin & B.A. Huber. 2013. Pholcid spider molecular systematics revisited, with new insights into the biogeography and the evolution of the group. *Cladistics* 29:132–146.
- Dunlop, J.A. & D. Penney. 2012. *Fossil Arachnida*. Siri Scientific Press, Manchester.
- Farris, J.S., V.A. Albert, M. Källersjö, D. Lipscomb & A.G. Kluge. 1996. Parsimony jackknife outperforms neighbor-joining. *Cladistics* 12:99–124.
- Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: Solutions for composite optima. *Cladistics* 15:415–428.
- Goloboff, P.A., J.S. Farris, M. Källersjö, B. Oxelman, M.J. Ramírez & C.A. Szumik. 2003a. Improvements to resampling measures of group support. *Cladistics* 19:324–332.

- Goloboff, P.A., J.S. Farris & K.C. Nixon. 2003b. TNT: Tree Analysis Using New Technology. Computer software and documentation. (Accessed May 2016.) Online at <http://www.lillo.org.ar/phylogeny/tnt/>
- Goloboff, P.A., J.S. Farris & K.C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786.
- Hadley, A. 2008. 'CombineZM'. (Accessed May 2016.) Online at <http://combinezm.en.lob4d.com/>
- Harvey, M.S. 2003. Catalogue of the smaller arachnid orders of the World: Amblypygi, Uropygi, Schizomida, Palpigradi, Ricinulei and Solifugae. CSIRO Publishing, Collingwood Victoria, Australia.
- Harvey M.S. & W.B. Muchmore. 2013. The systematics of the pseudoscorpion family Ideoroncidae (Pseudoscorpiones: Neobisioidea) in the New World. *Journal of Arachnology* 41:229–290. doi.10.1636/k13-42.1
- Harvey, M.S., O. Berry, K.L. Edward & G. Humphreys. 2008. Molecular and morphological systematics of hypogean schizomids (Schizomidae: Hubbardiidae) in semiarid Australia. *Invertebrate Systematics* 22:167–194.
- Lawrence, R.F. 1969. The trichoid structures on the chelicerae of the short-tailed whip-scorpions (Schizomida: Arachnida). *Transactions of the Royal Society of South Africa*. 38:123–132.
- Monjaraz-Ruedas, R. 2013. A new species of *Protoschizomus* (Schizomida: Protoschizomidae) from a cave in Guerrero, Mexico. *Journal of Arachnology* 41:420–424.
- Monjaraz-Ruedas, R., O.F. Francke & J.C. Cokendolpher. 2016a. Three new species of *Agastoschizomus* (Arachnida: Schizomida: Protoschizomidae) from North America. *Revista Mexicana de Biodiversidad* 87:337–346.
- Monjaraz-Ruedas, R., O.F. Francke, J.A. Cruz-López & C.E. Santibáñez-López. 2016b. Annuli and setal patterns in the flagellum of female micro-whipscorpions (Arachnida: Schizomida): Hypotheses of homology across an order. *Zoologischer Anzeiger* 263:118–134.
- Montaño-Moreno, M. & O.F. Francke. 2009. A new species of *Agastoschizomus* (Schizomida: Protoschizomidae) from Guerrero, Mexico. *Texas Memorial Museum Speleological Monographs, Studies on the Cave and Endogean Fauna of North America* 5:33–36.
- Morrone, J.J. 2005. Hacia una síntesis biogeográfica de México. *Revista Mexicana de Biodiversidad* 76:207–252.
- Nixon, K.C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15:407–414.
- Nixon, K.C. 2002. Winclada, version 1.00.08. Computer software and documentation. (Accessed May 2016.) Online at <http://www.cladistics.com>
- Petrunkovitch, A. 1955. Arachnida. Pp. 42–162. *In* Treatise on Invertebrate Paleontology. P, Arthropoda, Vol. 2. (R.C. Moore, ed.). University of Kansas Press, Lawrence, Kansas.
- Pierce, W.D. 1950. Fossil arthropods from onyx marble. *Bulletin of the Southern California Academy of Sciences* 49:101–104.
- Pierce, W.D. 1951. Fossil arthropods from onyx marble. *Bulletin of the Southern California Academy of Sciences* 50:34–49.
- Prendini, L. 2011. Order Schizomida Petrunkevitch, 1945. *In* Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness. (Z.Q. Zhang, ed.). *Zootaxa* 3148:156.
- Reddell, J.R. & J.C. Cokendolpher. 1995. Catalogue, bibliography, and generic revision of the order Schizomida (Arachnida). *Texas Memorial Museum, Speleological Monographs* 4:1–170.
- Rowland, J.M. 1975. A partial revision of Schizomida (Arachnida), with descriptions of new species, genus, and family. *Occasional Papers of the Museum, Texas Tech University* 31:1–21.
- Santibáñez-López, C.E., O.F. Francke & L. Prendini. 2014. Phylogeny of the North American scorpion genus *Diplocentrus* Peters, 1861 (Scorpiones: Diplocentridae) based on morphology, nuclear and mitochondrial DNA. *Arthropod Systematics & Phylogeny* 72:257–279.
- Vignoli, V. & L. Prendini. 2009. Systematic revision of the troglomorphic North American scorpion family Typhlochactidae (Scorpiones, Chactioidea). *Bulletin of the American Museum of Natural History* 326:1–94.
- Wiens, J.J. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. *Systematic Biology* 52:528–538.

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APPENDIX 1. Terminal taxa used for the cladistics analyses of 15 schizomid species of the family Protoschizomidae, and seven species of Hubbardiidae and 141 morphological characters. Material examined is deposited in the following collections: American Museum of Natural History (AMNH), New York, U.S.A.; Colección Nacional de Arácnidos, Instituto de Biología, Universidad Nacional Autónoma de México (CNAN), Mexico City, Mexico; Natural History Museum (NHM), London, England; Museum of Texas Tech University – Invertebrate Zoology (TTU-Z), Lubbock, U.S.A; and Texas Natural History Collections at the University of Texas at Austin (TMM). Coordinates in brackets are retrieved from Google Earth.

Outgroup

Megaschizomus mossambicus (Lawrence, 1958). MOZAMBIQUE: *Sofala*: Serra da Gorongosa (Mt Gorongosa), [18.4211°S, 34.1120°E 800 m.], September 1957, R. F. Lawrence. 1 female paratype (NHM).

Bamazomus sp. MADAGASCAR: Mangabe Island: Antogil Bay [15.4944°S, 49.7677°E, 268 m.], 19 February 1977, W. L. Brown. 1 male (AMNH).

Hubbardia borregoensis (Briggs & Holm, 1966). U.S.A.: *California*: San Diego County: Borrego Palm Canyon [33.2500°N, 116.3833°W, 232 m.], 12 January 1971, J.M. Rowland, T. Moisi. Two males, one female (AMNH).

Hubbardia pentapeltis Cook, 1899. U.S.A.: *California*: Orange County: Dripping Springs, near Yail Lake [33.7333°N, 117.6833°W, 397 m.], 6 March 1971, J. M. Rowland. 3 males, 5 females (AMNH).

Mayazomus infernalis (Rowland, 1975). MEXICO: *Chiapas*: Municipio Palenque, 0.8 km north of Ruinas de Palenque, [17.483839°N, 92.045353°W 154 m.], 25 July 1973, R. Mitchell and J. Reddell. 1 male holotype, 1 female allotype, 1 male, 3 female paratypes (AMNH). Convention Center of Ruinas de Palenque (17.3200°N, 92.0215°W 57 m.), 31 July 2013, O. Francke, J. Mendoza, R. Monjaraz, C. Santibáñez A. Valdez, K. Zarate. 1 male and 1 female (CNAN-Sz000122).

Rowlandius viridis (Rowland & Reddell, 1979a). JAMAICA: *Manchester Parish*: Abey Cave, 4 km. south-west of Mandeville, [18.008°N, 77.528°W, 751 m.], 24 December 1973, S. and J. Peck. male holotype, female allotype, 1 female and 3 female paratypes (AMNH).

Surazomus sturmi (Kraus, 1957). COLOMBIA: *Cundinamarca*: Distrito Capital, 3 km east of Bogota, [4.60°N, 74.08333°W, 2500 m.], October, 1956, H. Sturm. One female paratype (AMNH).

Ingroug

Agastoschizomus huitzmolotitlensis Rowland, 1975. MEXICO: *San Luis Potosí*: Xilitla, Sótano de Huitzmolotitla, 1 km ESE of Tlamaya

(=2 km NNW Xilitla), [21.408320°N, 99.0018°W, 600 m; depth in the cave where it was collected is unknown], 24 January 1964, T. Raines, T. Phillips, male holotype (AMNH).

Agastoschizomus juxtlahuacensis Montaña-Moreno and Francke, 2009. MEXICO: Guerrero, Quechultenango, Grutas de Juxtlahuaca, [17.4387333°N, 99.1595°W, 938? m.], 5 April 2007, H. Montaña, O. Francke, A. Valdez, C. Santibáñez, male holotype (CNAN-T0245), one adult male paratype (CNAN-T0246), one juvenile female paratype (CNAN-T0249).

Agastoschizomus lucifer Rowland, 1971. MEXICO: San Luis Potosí: Ciudad Valles, Sótano de la Tinaja, 10 km NNE of Ciudad Valles, [22.07597°N, 98.9778°W, 165.5 m.], 9 April 1966, J. Fish, D. McKenzie, male holotype, female paratype, 1 immature (AMNH). Ciudad Valles, Sótano de la Tinaja, 10 km NNE of Ciudad Valles, [22.07597°N, 98.9778°W, 165.5 m.], 11 May 2012, J. Cruz, J. Mendoza, G. Contreras, R. Monjaraz. One female (CNAN-Sz000136).

Agastoschizomus patei Cokendolpher and Reddell, 1992. MEXICO: Tamaulipas: Mainero, Cueva de la Llorona, 3.5 km SSE Yerbabuena, [24.4832°N, 99.599733°W, 1860 m.], 12-17 October 1986, P. Sprouse, male holotype (AMNH).

Agastoschizomus stygius Cokendolpher and Reddell, 1992. MEXICO: Hidalgo: Jacala, Sótano Hondo de Pinalito, Pinalito (a village located at kilometer post 105 on highway 85 north of Jacala), [21.01611°N, 99.164765°W, 1600 m.], 1 January 1976, C. Soileau, P. Strickland, female holotype (AMNH).

Agastoschizomus tamaulipensis Monjaraz-Ruedas, Francke & Cokendolpher, 2016. MEXICO: Tamaulipas: Municipio Ciudad Mante, Grutas de Quintero, 1.5 km S of Quintero (22.6499333°N, 99.041155°W, 452 m.), 27 November 2004, E. Fant, J. Fant holotype. Adult male (CNAN-T0983). Paratype: 1 subadult female (CNAN-T0984), 28 November 2004, same data as holotype.

Agastoschizomus tenebris Monjaraz-Ruedas, Francke & Cokendolpher, 2016. MEXICO: Estado de México: Valle de Bravo, Cueva del Diablo, Peña de Valle de Bravo (19.20069°N, 100.14148°W, 1885 m.), 27 August 2011, D. Barrales, J. Mendoza, E. Miranda, R. Monjaraz, A. Valdez, holotype. Adult female (CNAN-T0989). Paratype: 1 subadult female (CNAN-T0990), same data as holotype.

Agastoschizomus texanus Monjaraz-Ruedas, Francke & Cokendolpher, 2016. U.S.A.: Texas: Seminole Sink (= Seminole Canyon Cave), Seminole Canyon State Park, Val Verde County (415 m.), 20 February 2009, P. Paquin, M. Sanders, K. O'Connor, holotype adult female (TTU-Z_060311). Paratypes: 1 subadult male, (TTU-Z_060312), same data as holotype. 1 female and 1 subadult female (CNAN-T1002), same locality as holotype, 29 May 2015, P. Sprouse, B. Hutchins, and A. Scott.

Protoschizomus franckei Monjaraz-Ruedas, 2013. MEXICO: Guerrero: Taxco de Alarcón, Cueva de Boca del Diablo, Acuitlapán, [18.59916°N, 99.54579°W, 1594 m.], 21 April 2012, G. Contreras, J. Mendoza, R. Monjaraz, D. Ortiz, male holotype (CNAN-T0384), female paratype (CNAN-T0385).

Protoschizomus gertschi Cokendolpher and Reddell, 1992. MEXICO: Tamaulipas: Miquihuana, Sótano de Riachuelo, 6.5 km N. and 2 km E. of Miquihuana, [23.6333°N, 99.7819°W, 1850 m.], 16

February 1981, P. M. Jameson and R. Jameson. Female paratype (AMNH).

Protoschizomus occidentalis Rowland, 1975. MEXICO: Colima: 20.9 km SW Colima, [19.113469°N, 103.8571°W, 202 m.], 16 July 1972, A. Jung, male holotype (AMNH).

Protoschizomus pachypalpus (Rowland, 1973). MEXICO: Tamaulipas: Gómez Farías, Nacimiento del Río Frío, 3 miles S. of Gómez Farías, [23.070213°N, 99.147765°W, 450 m.], 12 March 1969, J. Reddell. Female holotype (AMNH).

Protoschizomus purificacion Cokendolpher and Reddell, 1992. MEXICO: Tamaulipas: Hidalgo, Cueva X, Conrado Castillo, [23.96311°N, 99.47554°W, 1950 m.], 27 December 1986, P. Sprouse, female holotype (AMNH); 15 April 1980, D. Pate, immature male paratype (TMM). *Protoschizomus treacyae* [new synonymy] - Cueva del Borrego, 0.5 km S of Conrado Castillo, [23.48333°N, 99.300°W, 1980 m.], 26 December 1986, Treacy Sprouse, female holotype (AMNH).

Protoschizomus rowlandi Cokendolpher and Reddell, 1992. MEXICO: San Luis Potosí: Ciudad Valles, 51.5 miles (82.9 km) E. of Ciudad Valles on Highway 70, [21.985355°N, 98.216481°W, 4 m.], 17 October 1972, B. Firstman, V. Roth. One male holotype and one female paratype (AMNH).

Protoschizomus sprousei Cokendolpher and Reddell, 1992. MEXICO: Tamaulipas: Güémez, Cueva del Tecolote, Los San Pedro, [23.959502°N, 99.474805°W, 1940 m.], 18 November 1984, P. Sprouse. One male holotype and one female paratype (AMNH).

APPENDIX 2. List of 138 morphological characters scored for the phylogenetic analyses of 15 protoschizomid species and seven outgroup hubardiids species. Characters from previous analyses that correspond partially or entirely to the present list (and in the matrix, Appendix 3) are indicated in brackets using the following abbreviations: C&R95 (Cokendolpher & Reddell, 1992) followed by the character number from the corresponding publication. Seven uninformative characters (excluded from all analyses) are indicated by †.

0. Chelicerae, mesal surface, setae G5, number: absent (0); ≤8 (1); ≥9 (2).
1. Chelicerae, mesal surface, movable finger, margin: smooth (0); with teeth (1).
2. Chelicerae, mesal surface, fixed finger, tooth, number: 2 (0); > 3 (1); 3 (2) [C&R95: 14].
3. Chelicerae, mesal surface, movable finger, serrula: rounded knobs (0); hyaline teeth (1) [C&R95: 15].
4. Cheliceral brush: absent (0); present (1) [C&R95: 16].
5. Propeltidium, size: small [1.06-1.26mm] (0); medium [1.36-1.52mm] (1); large [1.70-1.87mm] (2).
6. Propeltidium, anterior process, number of setae: one (0); row of two (1); 2+1 (2); without setae (3) [C&R95: 3].
7. Propeltidium, anterior process, pair of setae at the base: present (0); absent (1).
8. Propeltidium, pairs of dorsal setae: >2 (0); two anterior pairs (1); two separated pairs (2) [C&R95: 5].
9. Dorsoventral muscles, number: 8 (0); 7 (1) [C&R95: 29].
10. Metapeltidium, divided: absent (0); present (1).
11. Length of pedipalps compared to body length (♂): approximately same length (0); pedipalp longer than body (1); pedipalp shorter (2) [C&R95: 21].

12. Pedipalp, trochanter, mesal surface, number of setae near ventral margin: >4 (0); 3 (1).
13. Pedipalp, trochanter, mesal surface, setae: acuminate (0); spiniform (1).
14. Pedipalp, trochanter, mesal spur: absent (0); present (1).
15. Pedipalp, femur, ectal surface, seta Fev1: acuminate (0); spiniform (1); spiniform setiferous tubercle (2); macrosetae (3).
16. Pedipalp, femur, ectal surface, seta Fev2: acuminate (0); spiniform (1); spiniform setiferous tubercle (2); macrosetae (3).
17. Pedipalp, femur, ectal surface, seta Fe1: acuminate (0); spiniform (1); spiniform setiferous tubercle (2); macrosetae (3).
18. Pedipalp, femur, ectal surface, seta Fe2: acuminate (0); microseta (1); macrosetae (2).
19. Pedipalp, femur, ectal surface, seta Fe3: absent (0); present as acuminate (1); present as microseta (2).
20. Pedipalp, femur, ectal surface, seta Fe4: absent (0); present as acuminate (1); present as microseta (2).
21. Pedipalp, femur, ectal surface, seta Fe5, shape: acuminate (0); spiniform (1).
22. Pedipalp, femur, ectal surface, seta Fed1: absent (0); acuminate (1); microseta (2).
23. Pedipalp, femur, ectal surface, seta Fed2: absent (0); present, acuminate (1).
24. Pedipalp, femur, ectal surface, seta Fed3: acuminate (0); spiniform (1).
25. Pedipalp, femur, mesal surface, seta Fmv1: absent (0); present, macroseta (1); present, spiniform (2).
26. Pedipalp, femur, mesal surface, seta Fmv2: spiniform (0); acuminate (1); macroseta (2).
27. Pedipalp, femur, mesal surface, seta Fmv3: spiniform (0); acuminate (1); macroseta (2).
28. Pedipalp, femur, mesal surface, seta Fmv4: spiniform (0); acuminate (1); macroseta (2).
29. Pedipalp, femur, mesal surface, seta Fm1: absent (0); spiniform (1).
30. Pedipalp, femur, mesal surface, seta Fm2: absent (0); spiniform (1).
31. Pedipalp, femur, mesal surface, seta Fm3: absent (0); spiniform (1).
32. Pedipalp, femur, mesal surface, seta Fm4: absent (0); spiniform (1).
33. Pedipalp, femur, mesal surface, seta Fm5: absent (0); spiniform (1).
34. Pedipalp, femur, mesal surface, seta Fm6: absent (0); spiniform (1).
35. Pedipalp, femur, mesal surface, seta Fm7: absent (0); acuminate (1).
36. Pedipalp, femur, mesal surface, seta Fmd1: absent (0); present, acuminate (1); present, spiniform (2).
37. Pedipalp, femur, mesal surface, seta Fmd2: macroseta (0); acuminate (1); spiniform (2).
38. Pedipalp, femur, mesal surface, seta Fmd3: absent (0); acuminate (1); spiniform (2); macrosetae (3).
39. Pedipalp, Patella, ventral surface, seta Pe4, shape: acuminate (0); spiniform (1); feathered (2).
40. Pedipalp, Patella, ventral surface, seta Pm5, shape: acuminate (0); spiniform (1); feathered (2).
41. Pedipalp, Patella, ventral surface, seta Pme1: absent (0); present as acuminate (1); present as spiniform (2).
42. Pedipalp, Patella, ventral surface, seta Pmm3: absent (0); present as acuminate (1); present as spiniform (2); present as feathered (3).
43. Pedipalp, Patella, ventral surface, seta Pmm2: absent (0); present (1).
44. Pedipalp, Patella, ventral surface, seta Pmm1: absent (0); present (1).
45. Pedipalp, Patella, ventral surface, seta Pe3, shape: acuminate (0); spiniform (1).
46. Pedipalp, Patella, ventral surface, seta Pe2, shape: acuminate (0); spiniform (1).
47. Pedipalp, Patella, ventral surface, seta Pe1: absent (0); present as acuminate (1); present as spiniform (2).
48. Pedipalp, Patella, ventral surface, seta Pm4, shape: acuminate (0); spiniform (1); feathered (2).
49. Pedipalp, Patella, ventral surface, seta Pm3, shape: acuminate (0); spiniform (1); feathered (2).
50. Pedipalp, Patella, ventral surface, seta Pm2: absent (0); present as acuminate (1); present as spiniform (2); present as feathered (3).
51. Pedipalp, Patella, ventral surface, seta Pm1: absent (0); present (1).
52. Pedipalp, Tibia, ventral surface, external row of setae, seta 1, shape: acuminate (0); spiniform (1).
53. Pedipalp, Tibia, ventral surface, external row of setae, seta 2, shape: acuminate (0); feathered (1).
54. Pedipalp, Tibia, ventral surface, external row of setae, seta 3, shape: acuminate (0); spiniform (1).
55. Pedipalp, Tibia, ventral surface, external row of setae, seta 4: absent (0); present (1).
56. Pedipalp, Tibia, ventral surface, external row of setae, seta 4, shape: acuminate (0); spiniform (1).
57. Pedipalp, Tibia, ventral surface, external row of setae, seta 5: absent (0); present (1).
58. Pedipalp, Tibia, ventral surface, external row of setae, seta 5, shape: acuminate (0); spiniform (1).
59. Pedipalp, Tibia, ventral surface, external row of setae, seta 6: absent (0); present as spiniform (1).
60. Pedipalp, Tibia, ventral surface, external row of setae, size: same size (0); distal enlargement (1).
61. Pedipalp, Tibia, ventral surface, internal row of setae, seta 1, shape: acuminate (0); feathered (1); spiniform (2).
62. Pedipalp, Tibia, ventral surface, internal row of setae, seta 3, shape: acuminate (0); feathered (1).
- †63. Pedipalp, Tibia, ventral surface, internal row of setae, seta 4, shape: acuminate (0); feathered (1).
- †64. Pedipalp, Tibia, ventral surface, internal row of setae, seta 5: absent (0); present (1).
65. Pedipalp, Tibia, ventral surface, internal row of setae, seta 5, shape: acuminate (0); feathered (1).
- †66. Pedipalp, Tibia, ventral surface, internal row of setae, seta 6: absent (0); present (1).
67. Pedipalp, Tibia, ventral surface, internal row of setae, size: same size (0); distal enlargement (1); basal enlargement (2).
68. Pedipalp, Tibia, ventral surface, medial row of setae, seta 1, shape: spiniform (0); feathered (1).
69. Pedipalp, Tibia, ventral surface, medial row of setae, seta 2, shape: spiniform (0); feathered (1).
70. Pedipalp, Tibia, ventral surface, medial row of setae, seta 3, shape: spiniform (0); feathered (1).
71. Pedipalp, Tibia, ventral surface, medial row of setae, seta 4: absent (0); present (1).
72. Pedipalp, Tibia, ventral surface, medial row of setae, seta 4, shape: spiniform (0); feathered (1).
73. Pedipalp, Tibia, ventral surface, medial row of setae, seta 5: absent (0); present, feathered (1).
74. Pedipalp, Tibia, ventral surface, medial row of setae, size: same size (0); distal enlargement (1).
75. Pedipalp, Tibia, ventral surface, seta TM1, shape: acuminate (0); feathered (1).
76. Pedipalp, Tibia, ventral surface, seta TM2: absent (0); present (1).
- †77. Pedipalp, Tibia, ventral surface, seta TM2, shape: spiniform (0); feathered (1).
- †78. Pedipalp, Tarsus, spurs: symmetrical (0); asymmetrical (1).

79. Leg IV, Trochanter, length, in proportion with length of the femur: 1/2 (0); 1/3 (1) [C&R95: 25].
80. Leg IV, Femur, less than 4.8 times longer than high: less (0); more (1). [C&R92: 24]
81. Flagellum (♂), dorsoventrally compressed: not compressed (0); compressed (1).
82. Flagellum (♂), shape: bulbous (0); tubular (1); lanceolate (2).
83. Flagellum (♂), widened distally: absent (0); present (1). [C&R92: 37]
84. Flagellum (♂), stalks: present (0); absent (1). [C&R92: 38]
85. Flagellum (♂), ventro-lateral lobes: absent (0); present (1).
86. Flagellum (♂), ratio width/length: over 3x long as wide (0); less than 3x long as wide (1) [C&R92: 39].
87. Flagellum (♂), distal portion: rounded (0); pointed (1).
88. Flagellum (♂), seta Dm1, position respect to Vm1: anterior (0); posterior (1); at the same level (2).
89. Flagellum (♂), seta Dm2: present (0); absent (1) [C&R92: 34].
90. Flagellum (♂), seta Dm3: absent (0); present (1).
91. Flagellum (♂), seta Dm4, position respect to D12: anterior (0); posterior (1); at the same level (2).
92. Flagellum (♂), seta D11: absent (0); present (1).
93. Flagellum (♂), seta D11, position respect to Vm3: anterior (0); posterior (1); at the same level (2).
94. Flagellum (♂), seta D12, position respect to V11: at the same level (0); anterior (1); posterior (2).
95. Flagellum (♂), seta D13, position respect to V12: at the same level (0); posterior (1); anterior (2).
96. Flagellum (♂), seta D14: absent (0); present, macroseta (1); present, microseta (2).
97. Flagellum (♂), seta D14, position respect to D13: anterior (0); posterior (1); at the same level (2).
98. Flagellum (♂), seta Vm1, position respect to Vm2: at the same level (0); posterior (1); anterior (2).
99. Flagellum (♂), seta Vm4: present (0); absent (1) [C&R92: 35].
100. Flagellum (♂), seta Vm5: absent (0); present (1).
101. Flagellum (♂), seta Vm5, position respect to V11: at the same level (0); posterior (1).
102. Flagellum (♂), microsetae, dorso-anterior pair: absent (0); present (1).
103. Flagellum (♂), microsetae, antero-lateral pair: absent (0); present (1).
104. Flagellum (♀), annuli shape: wide (0); slender (1); absent (2).
105. Flagellum (♀), size: less than 2.9 (0); more than 3 (1).
106. Flagellum (♀), annuli a: absence (0); presence (1).
107. Flagellum (♀), annuli b: absence (0); presence (1).
108. Flagellum (♀), annuli c: absent (0); present (1).
109. Flagellum (♀), annuli d: absence (0); presence (1).
110. Flagellum (♀), annuli e: absence (0); presence (1).
111. Flagellum (♀), seta Dm1, position respect to Vm1: at the same level (0); posterior (1).
112. Flagellum (♀), seta Dm2: absent (0); present (1).
113. Flagellum (♀), seta Dm3: absent (0); present (1).
114. Flagellum (♀), seta Dm4: present (0); absent (1).
115. Flagellum (♀), seta Dm4, position respect to D12: anterior (0); posterior (1); at the same level (2).
116. Flagellum (♀), seta D11: absent (0); present (1).
117. Flagellum (♀), seta D11, position respect to Vm3: anterior (0); posterior (1); at the same level (2).
118. Flagellum (♀), seta D12, position respect to V11: at the same level (0); anterior (1); posterior (2).
119. Flagellum (♀), seta D13, position respect to V12: at the same level (0); posterior (1); anterior (2).
120. Flagellum (♀), seta D14, position respect to D13: anterior (0); posterior (1).
- †121. Flagellum (♀), seta Vm2: absent (0); present (1).
- †122. Flagellum (♀), seta Vm1, position respect to Vm2: at the same level (0); posterior (1); anterior (2).
123. Flagellum (♀), seta Vm4: absent (0); present (1).
124. Flagellum (♀), microsetae, number of pairs: 2 (0); 3 (1).
125. Spermathecae, number of lobes: 1 pair (0); 2 pairs (1); more than 2 pairs (2).
126. Spermathecae, Gonopod: absent (0); present (1).
127. Spermathecae, chitinized arch: absent (0); present (1).
128. Spermathecae, margins of the receptaculum: smooth with pits (0); lobed with pits (1); saw-toothed with pits (2) [C&R92: 43].
129. Spermathecae, Microtubulus: absent (0); present (1).
130. Spermathecae, bulbs: absent (0); present (1).
131. Spermathecae, symmetry between lobes: symmetrical (0); asymmetrical (1).
132. Spermathecae, lobes: straight (0); curved (1).
133. Spermathecae, lobes, size between lobes: same size (0); different size (1).
134. Tergite III, number of setae: 2 (0); 4 (1).
135. Sternites, setae patterns (♂): scattered or irregular rows (0); two distinct rows (1) [C&R92: 27].
136. Sternite VI, size: long (0); short (1) [C&R92: 28].

APPENDIX 3. Distribution of the 137 morphological characters (Appendix 2) among ingroup and outgroup taxa for the phylogenetic analysis of the schizomid family Protoschizomidae Rowland, 1975. Material examined is listed in Appendix 1. Character states are recorded as 0-3, unknown (?), or inapplicable (-).

Megaschizomus mossambicus

21211230010200111112212112000000011122200031101222311011111111111110011111011100001000011010?010?01101100111111011-10-101011011??0100010

Bamazomus sp.

21111121011010100010000100111000000001000100000100000000-0-001001001111110101110101001021010-010-0111111111000000010-210100?211110101010

Hubbardia pentapeltis

2011122101110111110000102000000000022112200112110000010100121111010011111010110101000021010-110-1111111111100100010-0101001211110101010

Hubbardia borregoensis

20111121011101111101100020000000000221021001120010000101001211110101111101110101001021010-110-1111111111100100010-010100?211110101010

Surazomus sturmi

1011111101111010001010000011100000000110010000000000000100-001110-00111110010-110101000021010-210-11101?1111000?00010-??01?0?100111000010

Rowlandius viridis

1111101101011011111000000011100000000110210011000000000-0-011110-021110-0011110001001021010-000-11111?1111100?00010-0101000111111011010

Mayazomus infernalis

10111011210110122210000100000000000220111000011120000101000110?011110-01011110101001021010-100-0111111111100000010-010100011111000010

Protoschizomus rowlandi

0000011010110003330010111122211110110322030011222101111111
0111111010001001011000001110110101010202111100101111010010
000121?000100110101

Protoschizomus occidentalis

0000001010110003330010111122211110110322000010222101111111
011111100000100101100002111000010121020201011?010?????????
1???000110110101

Protoschizomus sprousei

0000021000100003330000111122211110011032203011122211111111
1111111100010010110000211100001010001010111100101111011-
122001210000010111001

Protoschizomus franckei

0000011000100003330000111122211110110322000011222101111111
1111111000001110110000211100101010102020111100101111010110
1001210000110101001

Protoschizomus pachypalpus

0000001010110003330000111122201110111032200001002210111110-
0111111000011101011000001110110101000222111?100101111010110
0001010000110111101

Protoschizomus gertschi

00000210001?00033301101111222011110110322000011222101111111
0111111000111101011000????????????????????1010011111001000010
100000111110?1

Protoschizomus purificacion

00000110001?00033301101111222011100110322000011222101111111
01111110001111010110000?010?111210001020111100101111010210
20012110000111110?1

Agastoschizomus juxtlahuacensis

0000020000100003330110111122211111110320031111222301111111
1111111100010110110110201110111010122010111000101111011111
0201210000?????010

Agastoschizomus lucifer

00000200001000033300000111222011111100320001010222311111111
1111111100010110110110201110001010122210111100101111010011
220101000000010010

Agastoschizomus huitzmolotitlensis

00000200000000033300001111222011011120320031011222301111111
000111110000?1101101101011101011100211200-00?010?????????
????????????010

Agastoschizomus patei

00000200000000033301101111222011011120320031011122301111111
010111110000110101101101010101011222110010120000001010011
2011110000110000010

Agastoschizomus stygius

00000200000?00033321101111222011010120320031011222301111111
1101111100101111011011????????????????????0000001111011112012
100002100000?0

Agastoschizomus tamaulipensis

00000200101?00033301101111222011011110320031011222301111111
110111111000110101101102011101010102020111100100111010011
0001211???????-010

Agastoschizomus tenebris

00000200001?00033301101111222111111120320031011222301111111
000111110000111011011????????????????????001011110100112000-
100000000001?0

Agastoschizomus texanus

00000000101000033301101111222011111110320031011222301111111
01011110000011010110100?????11?1110120201111001001110101110
101210000000010110

Onychotelyphonus bonneri

?????????????0??
???0????????????????????1010?11?1?1?0????????????????